

PHYLOGENETIC TREES IN PLANT SYSTEMATICS

TOD F. STUESSY

Department of Botany, The Ohio State University, Columbus, OH 43210

ABSTRACT

Phylogenetic tree diagrams have been used for over a century to portray visually the estimated phylogeny of plant groups. These often accompany revisionary studies and usually summarize the classification and evolutionary relationships. Despite their widespread use, most trees do not show all possible relationships among the taxa, and frequently the relationships are shown in an ambiguous fashion. This hampers communication about the systematics of the group and makes comparisons of several different competing classifications for the same group difficult. A phylogenetic tree which shows all possible relationships is called a phylogram, and it contains information about (1) cladistics (branching patterns), (2) chronistics (time of divergence), (3) phenetics (over-all similarity and/or difference among extant taxa), and (4) patristics (total evolutionary change). Use of explicitly derived phylograms with high informational content in routine revisionary work is recommended. A method is presented for making a phylogram showing all four relationships using the genus *Lagascea* (Compositae) as a model.

Tree-like diagrams that represent the evolutionary history of groups of organisms, or phylogenetic trees, have been used for nearly a century in systematic biology (Voss, 1952). Ever since Darwin's (1859) *The Origin of Species by Means of Natural Selection*, phylogenetic trees have accompanied evolutionary studies to illustrate relationships. They have frequently been used with revisionary studies to summarize the affinities among taxa, especially within genera, and it is almost expected in modern work to find such diagrams. Phylogenetic trees not only summarize evolutionary information, but they also serve as stimuli for more detailed studies on the same groups. They provide visual inducement to test hypotheses of expressed relationships.

Despite widespread use of phylogenetic trees in plant systematics, many of the diagrams constructed have two faults: (1) the specific kinds of relationships or evolutionary information are not always clear; and (2) the manner in which the tree was constructed is usually not explicit. These differences hamper communication about the relationships expressed in the tree and also about the classification from which it is derived [e.g., Parenti's (1980) misinterpretation of certain aspects of Cronquist's (1960, 1966) system of classification of the land plants]. This becomes especially apparent in trying to compare different trees (or other tree-like diagrams) of the same group, e.g., of the angiosperms (Cronquist, 1968, 1981; Takhtajan, 1969; Stebbins, 1974; Dahlgren, 1975, 1977a, b; Thorne, 1976). These

problems interfere with resolving the differences among the diagrams (and classification) and do not serve as a proper stimulus for further work; in fact, an impasse often is reached.

The purposes of this paper, therefore, are to: (1) indicate clearly the different kinds of relationships that can be shown in a phylogeny; and (2) provide an example of an approach to developing a phylogeny of many relationships in the genus *Lagascea* (Compositae), which has been revised recently (Stuessy, 1978). A number of workers have touched on this subject previously (e.g., Lam, 1936; Sneath and Sokal, 1973; Sneath, 1974, 1975; Eldredge and Cracraft, 1980; Mayr, 1981; Nelson and Platnick, 1981). I believe, however, that a focused discussion on the positive effects of representing explicit relationships in phylogeny for the practicing plant systematist is needed at this time.

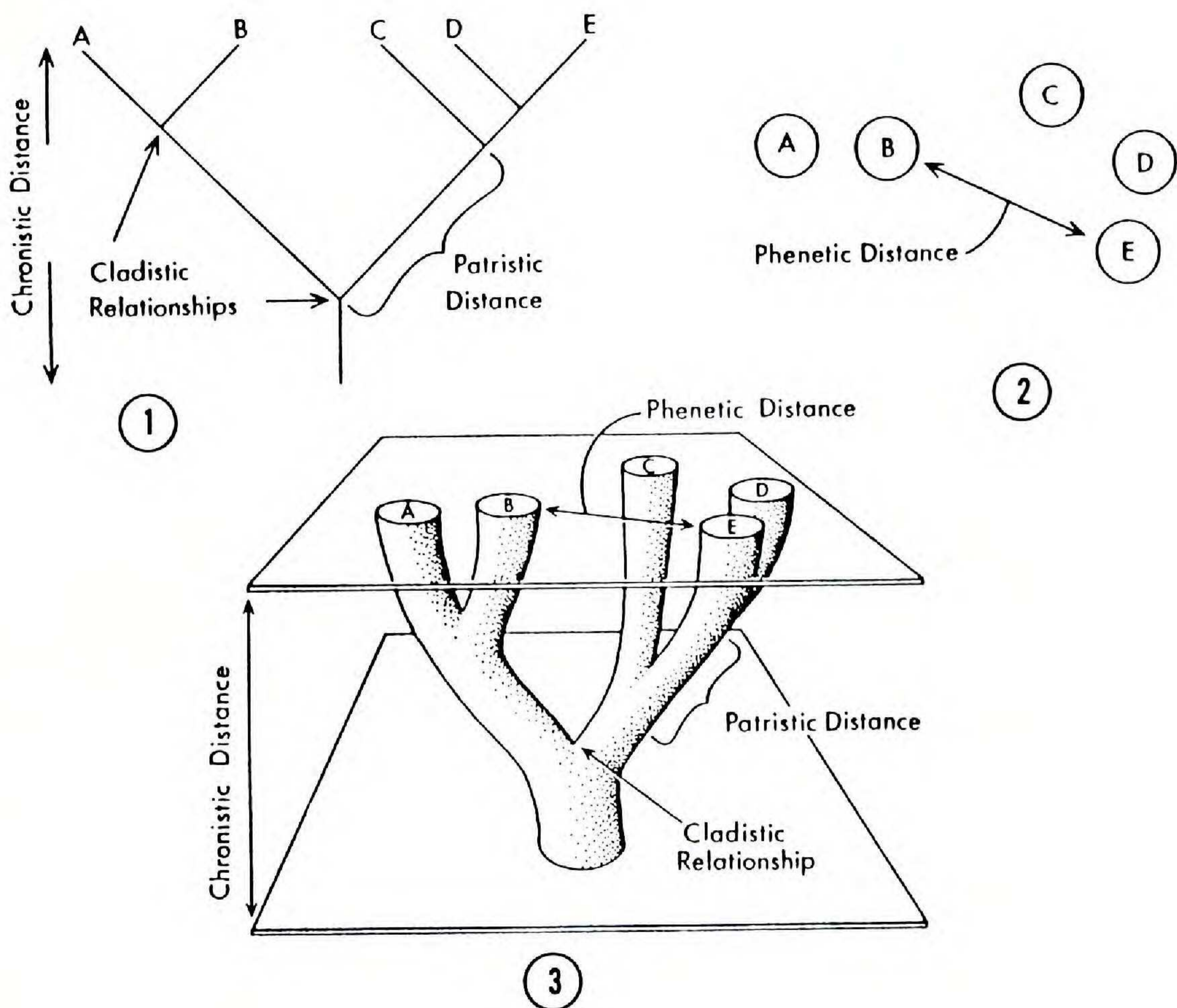
RELATIONSHIPS IN A PHYLOGENETIC TREE

To discuss the relationships that can be shown in a phylogenetic tree, it is important to stress that such tree diagrams have three dimensions¹. Within these three dimensions are represented four relationships: (1) chronistics; (2) cladistics; (3) patristics; and (4) phenetics.

CHRONISTICS.—The relationship of time is called chronistics. Obviously, all phylogenies have a time framework and this is measured usually in millions of years (Fig. 1). Time information can be derived directly from fossil evidence, or indirectly from extant distributional patterns. The former is self-evident, but the latter refers to vicariance events which can be explained by major geological alterations, for which geological age is known. Continental drift is a good example of this type of evidence which can help fix a time of origin (or splitting) of a lineage (cf. Nelson and Rosen, 1981, for many examples and perspectives).

CLADISTICS.—Cladistic relationships are the branching patterns of a phylogenetic tree, and therefore, are very important in any phylogenetic analysis (Fig. 1). This relationship, per se, says nothing about exactly where in geological time the branching took place, only that two (or sometimes more) lines diverge from a base of commonality of character states (primitive shared states for that line, but derived within the context of the entire tree; such derived states sometimes are called synapomorphies; Hennig, 1966). Cladistic relationships can be determined by many different manual or

¹ An effective, but unconventional and somewhat humorous, way to visualize a three-dimensional phylogenetic tree is to chop the flower buds off a fresh broccoli stem. The freshly cut terminal plane represents the present time and backwards down the stem successively younger phases of the phylogeny. Branching can be seen easily. For classroom use, one can actually ink the ends of the branches and press on blotter paper to get a view of phenetic relationships of present-day taxa. Successive planar cuts of the knife downward reveal the evolutionary appearance of the units and their relationships at earlier times.



Figs. 1-3. Diagrams showing relationships which can be expressed in an hypothetical phylogenetic tree (taxa A-E). Fig. 1, two-dimensional tree diagram showing chronistic, cladistic, and patristic relationships. 2, two-dimensional diagram showing phenetic relationships. 3, three-dimensional diagram (phylogram) combining chronistic, cladistic, patristic and phenetic relationships.

computer methods, but the two most common are those of parsimony and character compatibility (Funk and Stuessy, 1978). These all involve careful selection of characters and states (e.g., Crisci and Stuessy, 1980) and use of an algorithm (procedure) to actually draw the branching patterns.

PATRISTICS.—The patristic relationships are the total amounts of evolutionary changes along branches of the phylogenetic tree (Fig. 1). Cladistic relationships form the basis for determining patristic information, but in addition to the data of character state divergence due to splitting, are parallelisms and reversals that occur within each line (homoplasy; Simpson, 1961). In effect, the patristic relationships between taxa give additional relative indication of the degree of evolution within lineages, or whether some lines have evolved more rapidly than others. Cladistic and patristic

relationships, obviously, are closely tied together and the former analysis will be used to reveal the latter.

PHENETICS.—The phenetic relationship is the over-all similarity (or dissimilarity) of the taxa as we now would see them and intuitively assess their affinities (Sneath and Sokal, 1973). This can be diagrammed by envisioning we are looking at the end points of the lineage in the present time (Fig. 2) and the distance between these termini represents this over-all similarity. A number of methods can be used to develop this measure, but the most common are clustering and ordination (Sneath and Sokal, 1973). Because many characters are preferred for determining phenetic relationships (50 to 100), computers are usually employed to help with calculations.

These four relationships, chronistics, cladistics, patristics, and phenetics can all be represented on a single three-dimensional tree (called a "phylogram", Mayr, 1981; Fig. 3). This is the optimal situation in which information on all the four relationships is available. If all these data are not at hand, then at least the tree can be drawn to show clearly the relationships which are being incorporated (with clear and explicit figure legends). We are all familiar with the "diagrams showing evolutionary relationships" among taxa of certain groups, especially among species within genera that have been revised taxonomically, in which the dimensions or axes are unclear (e.g., Canne, 1977, her Fig. 7; Stuessy, 1977, his Fig. 1). Better would be for the relationships which were used to construct the phylogenetic tree to be stated more clearly (although sometimes this is difficult or impracticable). Another problem in tree construction, which has often occurred in the past, is that extant taxa are sometimes diagrammed as having given rise to other extant taxa (e.g., Takhtajan, 1969, his Fig. 31). This is simply "phylogenetic license" in tree construction, but it does make it impossible to show accurately chronistic and phenetic relationships (if known). Cladistic and patristic relationships, however, can still be shown accurately (e.g., see the phylogenetic tree for *Melampodium*; Stuessy, 1979, his Fig. 1). Such a phylogenetic tree is limited in communicating relationships and is better called a cladogram rather than a phylogram.

PHYLOGENY OF LAGASCEA (COMPOSITAE)

As an aid to understanding the concepts presented in the previous section of this paper, a phylogenetic tree of a small genus based on chronistic, cladistic, patristic and phenetic relationships will be constructed. The genus *Lagascea* Cav. (Compositae, Heliantheae) will be used for illustration. This taxon is a group of herbs and shrubs distributed almost exclusively along the Sierra Madre Occidental of Mexico (Stuessy, 1978). It is unusual within the Heliantheae in having secondary aggregations of unflowered capitula (Stuessy, 1976). These clusters are commonly surrounded by vegetative leaves which form a secondary involucre (the entire structure called a "syn-florescence"; Kunze, 1969). Stuessy (1978) in the most recent revision of

Lagascea recognized eight species grouped into three sections: Section *Lagascea*, *L. aurea* Stuessy, *L. mollis* Cav.; Section *Nocca*, *L. angustifolia* DC., *L. helianthifolia* H. B. K., *L. heteropappus* Hemsl., and *L. rigida* (Cav.) Stuessy; and Section *Calhounia*, *L. decipiens* Hemsl. and *L. palmeri* (Robins.) Robins. An intuitive phylogeny of the genus, incorporating explicit ideas on character evolution, was also presented. *Lagascea* is a good example to use in constructing a phylogenetic tree because: (1) it is a small, well-defined group; (2) the taxonomic relationships among the species and sections are clear and unambiguous; and (3) the genus *Alvordia*, used for outgroup comparisons, is well-understood (recently revised by Carter, 1964).

MATERIALS AND METHODS.—The characters used to determine phenetic and cladistic relationships in *Lagascea* were obtained primarily from the descriptions of species in the recent revision (Stuessy, 1978) with consultation of herbarium material (OS) where necessary for clarification. The quantitative data in the revision were described originally in terms of ranges of variation. For purposes here I used midpoints of the ranges to represent the states of all quantitative characters for each of the taxa. Maximum values were also used for comparison, but the results were the same and are not detailed here.

A total of 66 characters (18 vegetative and 48 reproductive) were used in assessing phenetic similarity. These characters are enumerated in Appendix I, along with the listing of each state, and the coding used in formulating the basic data matrix (Appendix II). The data matrix was analyzed using the BMDP computer program for factor analysis (P4M; Dixon and Brown, 1979).

In order to determine cladistic relationships within *Lagascea*, characters were selected for which it was possible to construct logical and unambiguous character state networks. Each network was then rooted by selecting the primitive character state of the network. The criterion used for determining which state was primitive was out-group comparison (Crisci and Stuessy, 1980), and *Alvordia* Brandg. was selected as the closest generic relative (Stuessy, 1976, 1977). The 16 characters used in the cladistic study, their states, and their numerical assignments are listed in Appendix I. Based on this information, which was incorporated into a basic data matrix (Appendix II), cladograms were formulated both manually (via Wagner Groundplan Divergence and Hennig-type methods; Mickel, 1962; Hennig, 1966; Wagner, 1980; Wiley, 1980) and with the Wagner 78 computer program (based on ideas in Farris, 1970).

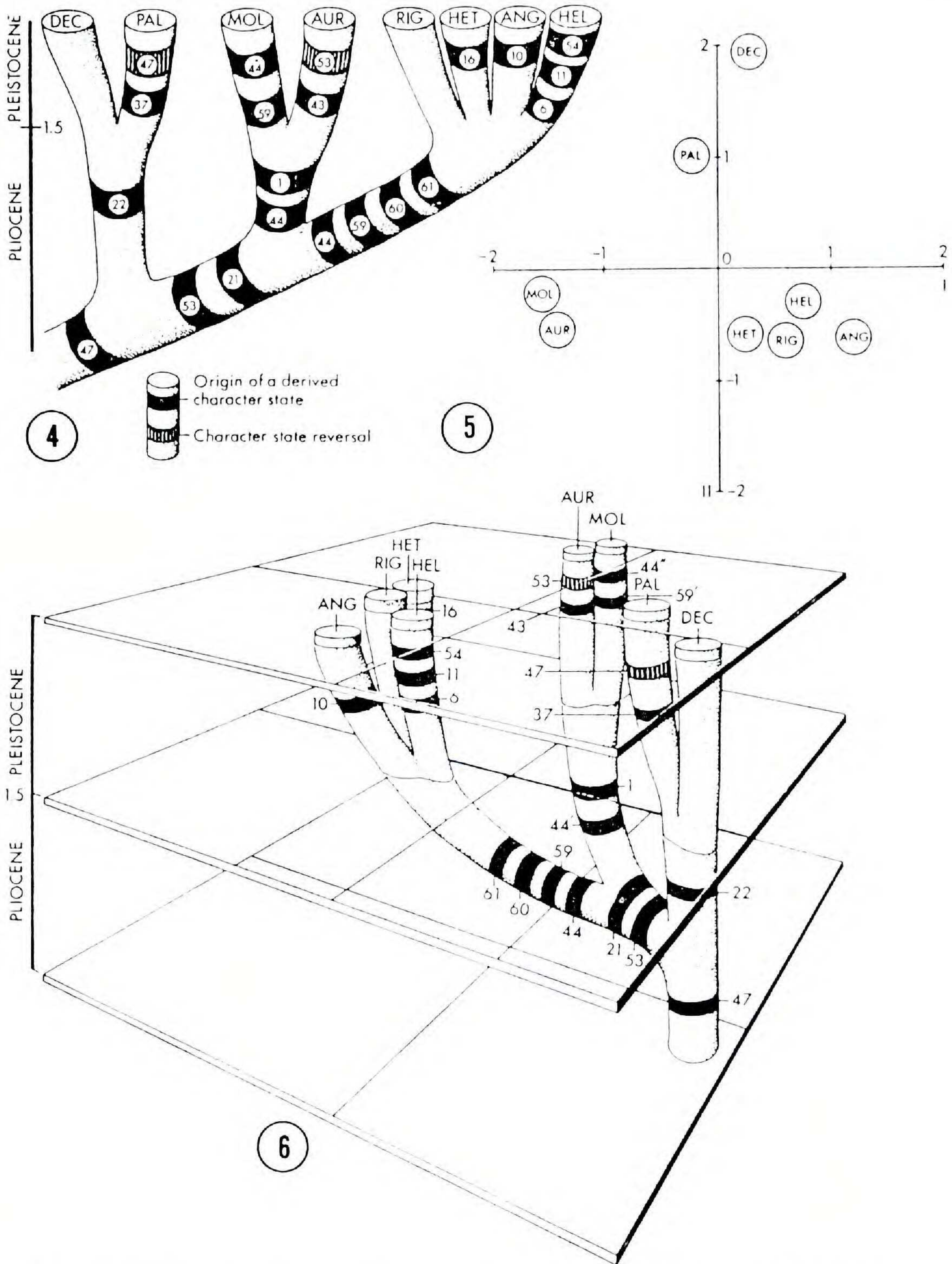
RESULTS.—The cladistic relationships of species of *Lagascea* are shown in Fig. 4. These branching patterns show clearly three main evolutionary lines which correspond to the previously recognized taxonomic sections. *Lagascea decipiens* and *L. palmeri* are shown to be closely related and these have been placed in Sect. *Calhounia*. These also show the fewest derived character state changes and may be regarded as the most primitive section

of the genus. *Lagascea mollis* and *L. aurea* form another distinct, but more advanced, evolutionary line. This corresponds with the previously recognized Sect. *Lagascea*. The four remaining species, *L. angustifolia*, *L. helianthifolia*, *L. heteropappus* and *L. rigida*, group together in the most advanced line and diverge from an unresolved tetrachotomy. These have been placed previously in Sect. *Nocca*. Three of the species (all but *L. helianthifolia*) are suspected of having been derived by adaptive radiation from within a broadly ranging taxon that was divided into three distinct populational systems, each eventually achieving specific status (Stuessy, 1978). The fourth species, *L. helianthifolia*, probably originated earlier and now has passed the test of sympatry (Mayr, 1942; Levin, 1971) by distributionally overlapping the related three taxa with only occasional hybridization (which happens due to breakdown in seasonal phenological isolation).

The patristic relationships are also shown in Fig. 4. The rings on the branches indicate changes in character states from primitive to derived conditions with no parallelisms and only two reversals (in characters 47 and 53). This is the most parsimonious tree that can be drawn from the data used. It becomes very clear that many features unite the sections within each of the lines, which are derived within the genus but primitive for the section. The branch leading to Sect. *Nocca* has more character state changes (4) than the rest, indicating that evolution has proceeded rapidly in this part of the phylogeny.

The chronistic relationships are also shown in Fig. 4 with the time dimension along the side of the tree. Because no mega- or micro-fossils are known for *Lagascea* (the entire fossil record of the family is still poorly understood; Crepet and Stuessy, 1978), the age of branch divergence must be determined by geological and/or distributional evidence. No data exist that help clarify the divergence of the pairs of species of Sects. *Calhounia* or *Lagascea*. Among the four species of Sect. *Nocca*, however, it is possible that *L. angustifolia*, *L. heteropappus*, and *L. rigida* were disrupted and isolated vicariously by the development of alluvial deposits of the Pliocene and Pleistocene in west-central Mexico (cf. Rzedowski, 1978; his Fig. 6 and Fig. 22 in Stuessy, 1978). If this were so (it is the only evidence presently available), then we might fix arbitrarily the age of divergence of these three species at about the Pleistocene-Pliocene boundary (1.5 million years ago). The age of divergence of the species in the other two lines cannot be determined independently, but the degree of cladistic (and phenetic, to be discussed below) distance between the pairs of species is comparable to that among the species of Sect. *Nocca*. It is unknown if the rate of character differentiation was the same (or at least similar) in each line, but we can arbitrarily fix the time of divergence for the species of these other lines at about the same point.

The phenetic relationships among species of *Lagascea*, as determined by factor analysis, is shown in Fig. 5. The three taxonomic sections stand out



Figs. 4-6. Cladistic, patristic, chronistic and phenetic relationships of *Lagascea*. Fig. 4, cladistic, patristic, and chronistic relationships. 5, phenetic relationships in a plot of the first two factors in factor analysis. 6, phylogenetic tree (phylogram) showing all four relationships. Arabic numerals in rings on branches in Figs. 4 and 6 refer to characters in which states have changed from primitive to derived conditions (or to reversals in 47 and 53). DEC = *L. decipiens*; PAL = *L. palmeri*; MOL = *L. mollis*; AUR = *L. aurea*; HEL = *L. helianthifolia*; RIG = *L. rigida*; HET = *L. heteropappus*; ANG = *L. angustifolia*.

clearly, and a close agreement exists with the results of the cladistic analysis. The distance in terms of over-all similarity² between any two taxa is shown, and the measure gives a good reflection of the way in which the species can be (and have been) differentiated and grouped intuitively. Another way of viewing this is how the diversity of *Lagascea* might appear to an observer in the present time plane (cf. broccoli model described earlier).

The cladistic, patristic, chronistic and phenetic relationships can be combined to produce a three-dimensional phylogenetic tree (phylogram) of *Lagascea* (Fig. 6). The phenetic relationships developed by factor analysis are used to determine the distance of the end points of the branches in the third dimension. The combination of phenetic and cladistic relationships in three dimensions gives a better visual representation of these parts of the phylogeny. This leads to a better understanding of the relative importance of these different measures of relationships for purposes of constructing a classification. In *Lagascea* a perfect graphic correlation exists between the cladistic and phenetic measures. In some groups this might not be the case, which would draw attention to the reasons for the differences.

CONCLUSION—The most important point of this paper is that the construction of phylogenetic trees can and should be done by explicit means. By determining the four relationships expressed in a phylogeny (cladistics, patristics, phenetics, and chronistics) and considering carefully how each can be graphically displayed, an increase in the communication of information about the final phylogeny occurs. Explicit methods and careful visual displays facilitate discussion about details of the phylogenetic reconstruction. Points of contention can more easily be addressed. In this fashion, the reconstructed tree serves as a greater stimulus for additional phylogenetic studies.

ACKNOWLEDGMENTS

Thanks go to: the Instructional and Research Computer Center of Ohio State University for computer time for the phenetic and cladistic analyses; students in Botany 810, Experimental Taxonomy, who provided helpful feedback on the ideas presented in this paper; David Dennis for drafting Figs. 1–7; NSF Grant DEB 75-20819 for financial support; and Michael Cichan and Vicki Funk for help with the early phases of the project.

REFERENCES

- CANNE, J. M. 1977. A revision of the genus *Galinsoga* (Compositae: Heliantheae). *Rhodora* 79: 319–389.

² One might question whether factor analysis represents over-all similarity in graphic display because suites of characters that account for maximum variation are selected and used for plotting of taxa on the coordinates. Nonetheless, the measure does begin with all characters and states and is routinely considered a phenetic technique (Sneath and Sokal, 1973; Clifford and Stephenson, 1975; McNeill, 1979). A clustering algorithm with two-dimensional graphic plot could also have been used here.

- CARTER, A. 1964. The genus *Alvordia* (Compositae) of Baja California, Mexico. Proc. Calif. Acad. Sci. 30: 157-174.
- CLIFFORD, H. T., and W. STEPHENSON. 1975. An introduction to numerical classification. Academic Press, N.Y.
- CREPET, W. L., and T. F. STUESSY. 1978. A reinvestigation of the fossil *Viguiera cronquistii* (Compositae). Brittonia 30: 483-491.
- CRISCI, J. V., and T. F. STUESSY. 1980. Determining primitive character states for phylogenetic reconstruction. Syst. Bot. 5: 112-135.
- CRONQUIST, A. 1960. The divisions and classes of plants. Bot. Rev. (Lancaster) 26: 425-482.
- _____. 1966. On the higher taxa of Embryobionta. Taxon 15: 129-134.
- _____. 1968. The evolution and classification of flowering plants. Houghton Mifflin Co., Boston.
- _____. 1981. An integrated system of classification of flowering plants. Columbia Univ. Press, N.Y.
- DAHLGREN, R. 1975. A system of classification of the angiosperms to be used to demonstrate the distribution of characters. Bot. Not. 128: 119-147.
- _____. 1977a. Ett angiospermschema och dess användning vid kartering av egenskaper. Svensk Bot. Tidskr. 71: 33-64.
- _____. 1977b. A commentary on a diagrammatic presentation of the angiosperms in relation to the distribution of character states. Plant Syst. Evolution Suppl. 1: 252-283.
- DARWIN, C. 1859. On the origin of species by means of natural selection. London.
- DIXON, W. J., and M. B. BROWN (eds.). 1979. BMDP-79: biomedical computer programs, P-series. Univ. Calif. Press, Berkeley.
- ELDREDGE, N., and J. CRACRAFT. 1980. Phylogenetic patterns and the evolutionary process: method and theory in comparative biology. Columbia Univ. Press, N.Y.
- FARRIS, J. S. 1970. Methods of computing Wagner trees. Syst. Zool. 19: 83-92.
- FUNK, V. A., and T. F. STUESSY. 1978. Cladistics for the practicing plant taxonomist. Syst. Bot. 3: 159-178.
- HENNIG, W. [transl. D. D. DAVIS and R. ZANGERL]. 1966. Phylogenetic systematics. Univ. Illinois Press, Urbana.
- KUNZE, H. 1969. Vergleichend-morphologische Untersuchungen an komplexen Compositen-Blütenständen. Beitr. Biol. Pflanzen 46: 97-154.
- LAM, H. J. 1936. Phylogenetic symbols, past and present. Acta Biotheor. 2: 155-194.
- LEVIN, D. A. 1971. The origin of reproductive isolating mechanisms in flowering plants. Taxon 20: 91-113.
- MAYR, E. 1942. Systematics and the origin of species. Columbia Univ. Press, N.Y.
- _____. 1981. Biological classification: toward a synthesis of opposing methodologies. Science 214: 510-516.
- McNEILL, J. 1979. Purposeful phenetics. Syst. Zool. 28: 465-482.
- MICKEL, J. T. 1962. A monographic study of the fern genus *Anemia*, subg. *Coptophyllum*. Iowa State Coll. J. Sci. 36: 349-383.
- NELSON, G., and N. PLATNICK. 1981. Systematics and biogeography: cladistics and vicariance. Columbia Univ. Press, N.Y.
- _____, and D. E. ROSEN. 1981. Vicariance biogeography: a critique. Columbia Univ. Press, N.Y.
- PARENTI, L. R. 1980. A phylogenetic analysis of the land plants. J. Linn. Soc. Biol. 13: 225-242.
- RZEDOWSKI, J. 1978. Vegetación de Mexico. Editorial Limusa, Mexico, D. F.
- SIMPSON, G. G. 1961. Principles of animal taxonomy. Columbia Univ. Press, N.Y.
- SNEATH, P. H. A. 1974. Phylogeny of microorganisms. Symp. Soc. Gen. Microbiol. 24:1-39.

- _____. 1975. Cladistic representation of reticulate evolution. *Syst. Zool.* 24: 360–368.
- _____, and R. R. SOKAL. 1973. *Principles of numerical classification*. W. H. Freeman, San Francisco.
- STEBBINS, G. L. 1974. *Flowering plants: evolution above the species level*. Harvard Univ. Press, Cambridge.
- STUESSY, T. F. 1976. A systematic review of the subtribe *Lagasceinae* (Compositae, Heliantheae). *Amer. J. Bot.* 63: 1289–1294.
- _____. 1977. Heliantheae—systematic review, pp. 621–671. *In*, V. H. Heywood, J. B. Harborne, and B. L. Turner (eds.), *The Biology and Chemistry of the Compositae*. Academic Press, London.
- _____. 1978. Revision of *Lagascea* (Compositae, Heliantheae). *Fieldiana Bot.* 38: 75–133.
- _____. 1979. Cladistics of *Melampodium* (Compositae). *Taxon* 28: 179–195.
- TAKHTAJAN, A. [transl. C. JEFFREY]. 1969. *Flowering plants: origin and dispersal*. Oliver & Boyd, Edinburgh.
- THORNE, R. F. 1976. A phylogenetic classification of the Angiospermae, *Evol. Biol.* 9: 35–106.
- VOSS, E. G. 1952. The history of keys and phylogenetic trees in systematic biology. *J. Sci. Lab. Denison Univ.* 43(1): 1–25.
- WAGNER, W. H., Jr. 1980. Origin and philosophy of the Groundplan-divergence method of cladistics. *Syst. Bot.* 5: 173–193.
- WILEY, E. O. 1980. Phylogenetic systematics and vicariance biogeography. *Syst. Bot.* 5: 194–220.

Appendix I. Characters and states of species of *Lagascea* used in the phenetic and cladistic analyses. All characters (except #6) were used for the phenetic analysis; characters in small capitals are those used also in the cladistic analysis, in which case 0 = primitive and 1 (or 2 and 3) = derived. All quantitative measurements are in mm unless stated otherwise.

1; HABIT, shrub (0), herb (1). 2, PLANT HEIGHT (m). 3, STEM Diam; 4, Color, yellow (0), green to gray (1); 5, Vesture, subglabrous to glabrous (0), pilose, hirtellous or strigose (1), sericeous (2). 6, LEAVES, petiolate (0), sessile (1). 7, PETIOLE LENGTH; 8, Diam; 9, Vesture, absent (0), ciliate or hirtellous (1). 10, BLADE SHAPE, ovate to narrowly ovate (0), lanceolate to oblanceolate (1); 11, LENGTH (cm); 12, Width (cm); 13, Apex, acute (0), acute-acuminate (1), acuminate (2); 14, Base, attenuate (0), attenuate-obtuse (1), obtuse to subauriculate (2); 15, Margin, subentire-serrate (0), serrate or serrate-dentate (1); 16 VESTURE (ABAXIAL), glabrous to subglabrous (0), strigose to tomentose (1), sericeous (2) [for cladistics the 1st 2 states coded as 0 and 2 as 1]; 17, Vesture (abaxial) Length; 18, Vesture (adaxial), as in 16; 19, Vesture (adaxial) Length. 20, SYNFLORISCENCE Number of Heads; 21, FLORETS/HEAD, sometimes 2-many (0), always 1 (1); 22, ARRANGEMENT, campanulate (0), globose (1); 23, Height (cm); 24, Diam (cm). 25, PEDUNCLE Length; 26, Diam; 27, Vesture, glabrous (0), strigose (1), sericeous (2), stipitate-glandular (3); 28, Vesture Length; 29, RECEPTACLE Diam; 30, Height; 31, Vesture, subglabrous (0), pubescent, hirtellous or pilose (1); 32, Vesture Length. 33, SECONDARY PHYLLARY Number; 34, Shape, lanceolate (0), lanceolate-ovate (1), lanceolate-obovate (2); 35, Length; 36, width; 37, VESTURE (ABAXIAL), strigose or pilose (0), stipitate-glandular (1), glabrous or subglabrous (2), [for cladistics the first 2 states coded as 0 and the third as 1]; 38, Vesture (abaxial) Length; 39, Vesture (adaxial), as in 37; 40, Vesture (adaxial) Length. 41, PRIMARY INVOLUCRE Length; 42, Diam; 43, NUMBER OF PHYLLARIES

[for cladistics 4-5 as 0, 6 as 1]; 44, NUMBER OF GLANDS/PHYLLARY [for cladistics 1 large gland (0), 3 medium glands in 1 row (1), more than 3 glands in 1 row (2), more than 3 glands each in 2-3 rows (3) *]; 45, Number of Rows of Glands; 46, Gland Length; 47, VESTURE (ABAXIAL), glabrous or subglabrous (0), strigose to pilose (1); 48, Vesture (abaxial) Length; 49, Vesture (adaxial), as in 47; 50, Lobe Length; 51, Lobe Width (base); 52, Apex, acute (0), acuminate (1). 53, COROLLA COLOR, yellow (0), pink or white (1); 54, THROAT LENGTH [for cladistics 2.8-5 mm (0), > 5 (1)]; 55, Throat Diam; 56, Lobe Length; 57, Tube Length; 58, Tube Diam. 59, ANTHOR COLOR, yellow (0), brown or black (1) [for cladistics brown (1), black (2) **]; 60, LENGTH [for cladistics 2-3 mm (0), 4.5-5 (1)]. 61, STYLE LENGTH [for cladistics 5-8 mm (0), 15-18 (1)]. 62, ACHENE Shape, cylindrical (0), obovate (1); 63, Length; 64, Diam. 65, PAPPUS Type, erose crown (0), awns (1); 66, Length.

* The character state tree for this character shows 0 giving rise to 1 in one direction and 2 and 3 sequentially in the other.

** The character state tree has 0 giving rise to 1 in one direction and 2 independently in the other.

Appendix II. Basic Data Matrix of states of characters in species and sections of *Lagascea*. See Appendix I for descriptors and numerical assignments of characters and states. If phenetic differs from cladistic coding, fractions are given with numerator the former and denominator the latter. Characters used for cladistic analysis italicized (these were also used for phenetic analysis, except for #6).

CHARACTERS	TAXA							
	Sect. <i>Lagascea</i>	Sect. <i>Nocca</i>			Sect. <i>Calhounia</i>			
	1. <i>L. mollis</i> Cav.	2. <i>L. aurea</i> Stuessy	3. <i>L. belianthifolia</i> H. B. K.	4. <i>L. rigida</i> (Cav.) Stuessy	5. <i>L. heteropappus</i> Hemsl.	6. <i>L. angustifolia</i> DC.	7. <i>L. decipiens</i> Hemsl.	8. <i>L. palmeri</i> (Robins.) Robins.
1	1	1	0	0	0	0	0	0
2	1	1	3	2	2	1.5	3	3
3	5	4.5	20	18	12	14	12	15
4	0	0	1	1	1	1	1	1
5	0	1	1	0	2	1	0	0
6	0	0	1	0	0	0	0	0
7	16	17.5	0	5	7	9.5	9	11
8	0.5	0.7	0	2	1.5	1.5	0.7	1
9	1	1	0	0	0	0	0	0
10	0	0	0	0	0	1	0	0
11	5.7	3.8	23.5	7.2	6.8	6.3	2.9	6.5
12	3.2	2.5	8.3	4.1	2.6	2.1	3.7	2.6

Appendix II. Continued
TAXA

CHARACTERS	1	2	3	4	5	6	7	8
63	3	2.8	5.5	4	3.3	4.5	3	3
64	1.2	1.1	1.2	1.2	1.3	1.3	0.8	0.5
65	0	0	1	1	1	1	0	0
66	0.2	0.3	0.5	1.8	1	0.8	0.1	0.2